

TAIL MUSCLE ACTIVITY PATTERNS IN WALKING AND FLYING PIGEONS (*COLUMBA LIVIA*)

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Summary

The electrical activity of major caudal muscles of the pigeon (*Columba livia*) was recorded during five modes of aerial and terrestrial locomotion. Tail muscle electromyograms were correlated with movement using high-speed cinematography and compared to activity in selected muscles of the wings, legs and trunk. During walking, the pectoralis and most tail muscles are normally inactive, but levator muscle activity alternates with the striding legs. In flight, caudal muscles are phasically active with each wingbeat and undergo distinct changes in electromyographic pattern between liftoff, takeoff, slow level flapping and landing modes. The temporal flexibility of tail muscle activity differs significantly from the stereotypic timing of wing muscles in pigeons performing the same flight modes. These neural programs may represent different solutions to the control of flight surfaces in the rapidly oscillating wing and the relatively stationary caudal skeleton. Birds exhibit a novel alliance of tail and forelimb use during aerial locomotion. We suggest that there is evidence of anatomical and functional decoupling of the tail from adjacent hindlimb and trunk muscles during avian evolution to facilitate its specialization for rectricial control in flight.

Introduction

The demand for coordination of all flight surfaces has yielded a specialized integration of the avian neuromuscular system. Although the majority of avian flight studies have focused on the wings, the tail also appears to be crucial to the evolutionary success of birds as flying organisms. Despite recent advances in our understanding of wing muscle activity and function (e.g. Dial *et al.* 1987, 1988, 1991; Jenkins *et al.* 1988; Dial, 1992*a,b*), the motor control of the avian tail during locomotion has remained unexplored.

Hypotheses of caudal muscle function are based on anatomical information (Fisher, 1946; Owre, 1967; Raikow, 1970, 1985; Baumel, 1988), qualitative descriptions of tail movement during flight (Brown, 1948; Pennycuick, 1968) or data from anesthetized (Baumel *et al.* 1990), restrained (Biederman-Thorson and Thorson, 1973; Bilo and Bilo, 1983) or surgically impaired (Fisher, 1957) birds. However, information is lacking on basic activity patterns of muscles controlling tail movement. This paper reports on the

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electrical activity of six major tail muscles of the pigeon during locomotion. We used electromyography (EMG) in conjunction with high-speed cinematography to record activity patterns of pigeon muscles during walking and four modes of symmetrical (i.e. non-turning) forward flight. These patterns are referenced to the activity in representative forelimb, hindlimb and trunk muscles.

Our results on freely locomoting pigeons are the first quantitative data available for the neural control of the tail in a vertebrate during flight. In view of recent studies of pigeon tail morphology (Baumel, 1988) and caudal muscle activity during ventilatory movements (Baumel *et al.* 1990), these EMG data provide a crucial test of predictions of tail muscle locomotor function. A basic description of this type is necessary for a more informed interpretation of results from reduced preparations (reflex studies, spinal transections, fictive locomotion, etc.) and data from more complex locomotor behaviors such as maneuvering flight. Finally, an understanding of caudal function is an essential step towards integrating both the wing and the tail into a more complete model of avian flight.

Materials and methods

Ten adult wild type pigeons (*Columba livia* Gmelin) with a mean body mass of 334 g (± 49 g, s.d.) were used in thirteen electromyographic (EMG) experiments. Birds were collected from local populations, housed in stainless-steel cages (1 m \times 1 m \times 1.5 m) and provided with commercial pigeon feed, vitamins and water *ad libitum*.

Locomotor modes

Birds were trained to fly onto an elevated perch-platform when either released from the hand or placed on the ground for unassisted takeoffs (Dial, 1992*a,b*). The flight corridor was 3.1 m wide, 2.7 m high and 50 m long. In this study we present data from five modes of locomotion: (1) walking, (2) liftoff, (3) takeoff, (4) slow level flapping flight and (5) landing (Fig. 1). Walking birds moved freely upon the floor of the flight corridor. Liftoff is a transitional mode between terrestrial and aerial locomotion. Here, liftoff is defined as the first wingbeat and associated leg thrust of an ascent from the ground. Takeoff is designated as the first five wingbeats subsequent to liftoff, during which birds were gaining altitude and forward velocity. Slow level flapping flight (Brown, 1948, 1963) is achieved after birds have attained maximum speed and fly level (for a distance of 15–20 m) down the corridor. Landing is defined as the last 5–7 wingbeats prior to touchdown on the perch-platform.

Anatomy and terminology

The morphology of the tail and pelvis was studied in fresh, frozen and preserved specimens ($N=6$) using a Wild M7-S binocular dissecting microscope. The epaxial musculature of the tail has been divided into two separate muscles by past workers (levator coccygis and levator caudae). In this paper we follow the newly revised terminology of Baumel *et al.* (1993), in which the caudal epaxials are considered as two parts (pars vertebralis and pars rectricalis) of a single muscle, the levator caudae. We

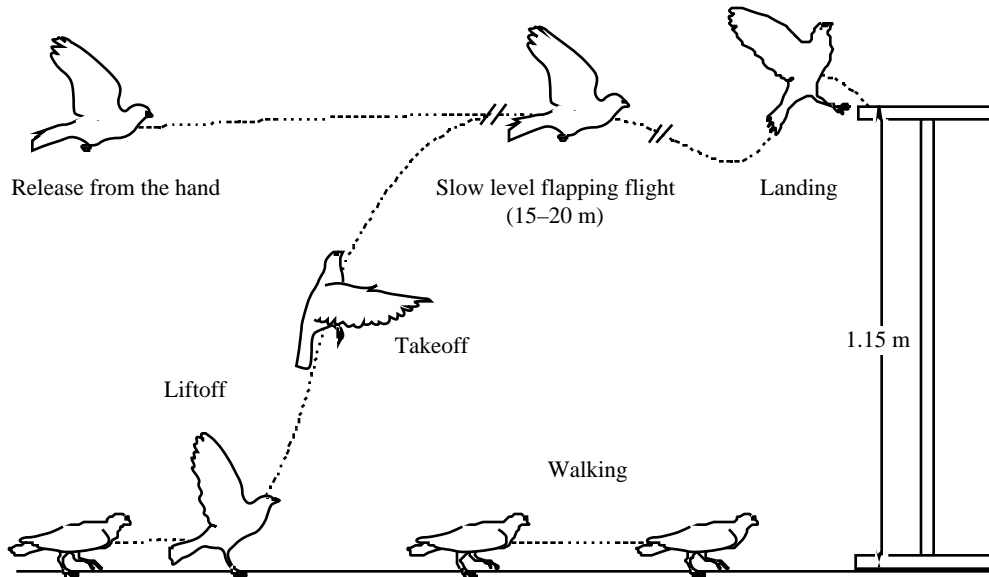


Fig. 1. Scheme of pigeon locomotion for recording muscle activity during walking, liftoff, takeoff, slow level flapping flight and landing locomotor modes. Note that the length of the flight corridor has been compressed. Typically, flights included 15–20m of slow level flapping between release or takeoff and landing on the perch.

recorded EMGs from the two parts of the levator caudae separately and treat them independently in our results.

Electromyography

Electromyographic data were gathered using surgically implanted bipolar electrodes similar to those previously described (Dial *et al.* 1988; Dial, 1992*a,b*). Birds were administered intramuscular doses of ketamine (25mgkg^{-1}) and xylazine (2mgkg^{-1}) to induce deep anesthesia during all surgical procedures. Injections were distributed around the body to avoid irritating muscles under study and supplementary amounts were given as needed. Feathers were plucked from four regions: (1) the middle of the back to accommodate a connector plug, (2) the left thoracic region to expose the pectoralis muscle, (3) the left side of the synsacrum to provide access to the hindlimb and trunk muscles, and (4) the base of the tail. The rectrices and most tail coverts were left intact. Electrodes ran subcutaneously from the female back plug (12-pole, consisting of two Microtech FG-6 miniature connectors), which was sutured to the thoracic interspinous ligaments. Target muscles were exposed by skin incisions and blunt dissection and then implanted with electrodes (twisted pairs of $100\ \mu\text{m}$ diameter silver wire with 0.5mm insulation removed at each recording tip and offset 1mm) using a 23-gauge hypodermic needle. Electrodes were sutured to adjacent periosteum or fascia approximately 1–5mm from their exit from the muscle. A short loop of wire was left between the exit point and suture to allow the electrode tips to move freely with the contracting muscle, significantly reducing low-frequency movement artifact from EMG signals.

EMG recordings were made on the first postoperative day. A 25m, lightweight, 12-lead shielded cable (Cooner Wire Co., Part no. NMUF 4/30-4046SJ) with a male miniature connector transmitted the signals to the recording equipment. The cable was taped to the bird's back and flank so that it passed over the right thigh beneath the tail, thus minimizing interference with locomotor movements. EMG signals were amplified and filtered (Grass P511J; 2000–20000 \times ; 100–3000Hz bandpass) before being simultaneously recorded on a four-channel Hewlett-Packard 3694A tape recorder at 15inches s^{-1} and to an eight-channel, 12-bit A/D converter (Keithley DAS 5000 series; 2040Hz sampling rate) for storage on a Zenith 386SX microcomputer. Data were printed on a Gould 2400 chart recorder and a Graphtec WR4000 thermal array recorder.

Eleven muscles were chosen for electromyographic recording. The pectoralis, the primary flight muscle, was implanted to monitor wing activity. The ilioprochantericus caudalis, a hip muscle, served as an indicator of hindlimb use. The pectoralis, ilioprochantericus caudalis and four additional muscles were sampled in most experiments. The caudofemoralis is a hindlimb muscle (based on its embryology; Romer, 1927), but originates from the tail and may be involved in caudal control. The longissimus dorsi provided information on epaxial muscle activity in the trunk. Two epaxials (levator caudae pars vertebralis and pars rectorialis) and five hypaxials (lateralis caudae, bulbi rectorium, depressor caudae, pubocaudalis externus and pubocaudalis internus) were recorded in the tail. Activity was recorded in the ventral fibers of the bulbi rectorium. The depressor caudae was implanted in its distal part, as exposed laterally, ventral to the caudal transverse processes; activity in the proximal and deep parts was not recorded. The pubocaudalis internus is a digastric muscle of which we sampled the pelvic head only. Electrode positions were verified by surgical removal or *post-mortem* dissection (in at least one bird for each muscle) following recording.

Cinematography

Simultaneous high-speed films were made of approximately half of the recorded EMG sequences. The camera (16mm Lo-Cam, Red Lakes Laboratories) ran at 150–200frames s^{-1} for flight and at 50frames s^{-1} for walking. An electrical pulse synchronized with each frame of film (Kodak 7250 Ektachrome) was recorded on tape and computer to permit correlation of kinematic and EMG data. Films were viewed using an L-W Motion Analyzer projector (model 224-S) to verify wing and leg position and to characterize tail movements qualitatively. Tracings were made from projected images of one bird during liftoff, takeoff, slow level flight and landing.

Data analysis

For analysis of the motor pattern of the recorded muscles, EMG signals were displayed from the stored digital data on a Tektronix 4109 graphics terminal. Signals were digitally rectified prior to measuring timing of activity using custom digitizing programs supplied by G. V. Lauder. Each muscle was analyzed to determine onset and offset times relative to a reference muscle (pectoralis during flight and ilioprochantericus caudalis during walking). EMG bursts were identified as changes in amplitude at least two times greater than baseline. Most EMGs were discrete bursts with amplitudes well above background

Table 1. Duration and frequency of stride and wingbeat cycles in pigeons during five modes of locomotion

Locomotor mode	Mean duration (ms)	s.D. (ms)	<i>N</i>	Minimum (ms)	Maximum (ms)	Mean frequency (Hz)	s.D. (Hz)
Walking	409.5	77.8	35	210	551	2.55	0.63
Liftoff	105.3	5.2	25	96	115	9.52	0.48
Takeoff	110.7	6.9	55	96	130	9.07	0.58
Slow LFF	122.6	9.3	55	103	151	8.20	0.61
Landing	122.8	10.2	50	88	152	8.20	0.73

LFF, level flapping flight.

activity (see Figs 7–9). Timing was measured at a resolution of 0.5ms. These data were then normalized to each wingbeat or stride in order to compare activity within a locomotor cycle between different birds. Mean cycle duration and frequencies are given in Table 1. Five cycles from each of two birds were averaged for each muscle within each mode of locomotion, with the exception of liftoff. Liftoff sample sizes were: pectoralis (25 liftoffs, 7 birds), iliотrochantericus caudalis (17, 4), caudofemoralis (6, 2), longissimus dorsi (7, 2), levator caudae pars vertebralis (12, 2), levator caudae pars rectorialis (7, 2), lateralis caudae (10, 3), bulbi rectorium (1, 1), depressor caudae (6, 2), pubocaudalis externus (7, 3) and pubocaudalis internus (9, 3).

Results

Anatomy

Only a general description of caudal myology is presented here (Fig. 2; see Baumel, 1988, for a thorough study of pigeon tail anatomy). The tail skeleton is composed of five or six free caudal vertebrae and a terminal pygostyle. Six pairs of main tail feathers (rectrices) are rooted in a fibroadipose structure called the rectricial bulb (Baumel, 1988). Major movements of the tail feathers are controlled by muscles connecting the synsacrum, pelvis, femora and caudal vertebrae to the tail skeleton and rectricial bulbs.

One noteworthy characteristic of the avian tail is its relative isolation from surrounding trunk and hindlimb structures. Dorsally, the epaxial musculature of the trunk (longissimus dorsi) is not continuous with the adjacent epaxial musculature of the tail (levator caudae pars vertebralis). Between these muscles, dorsal rami of spinal nerves perforate the synsacrum but do not supply motor innervation. In the pigeon this hiatus spans at least four spinal levels. Laterally, the caudal musculature has almost no overlap with the muscles of the hind legs; both take origin from the fused pelvic bones. The one exception is the caudofemoralis muscle, which runs from the base of the pygostyle to the femur. Posteriorly, the eminence of the vent is connected to the tail by the septum supracloacale and the slender levator cloacae muscles. The influence of cloacal muscles on the tail during flight remains unknown.

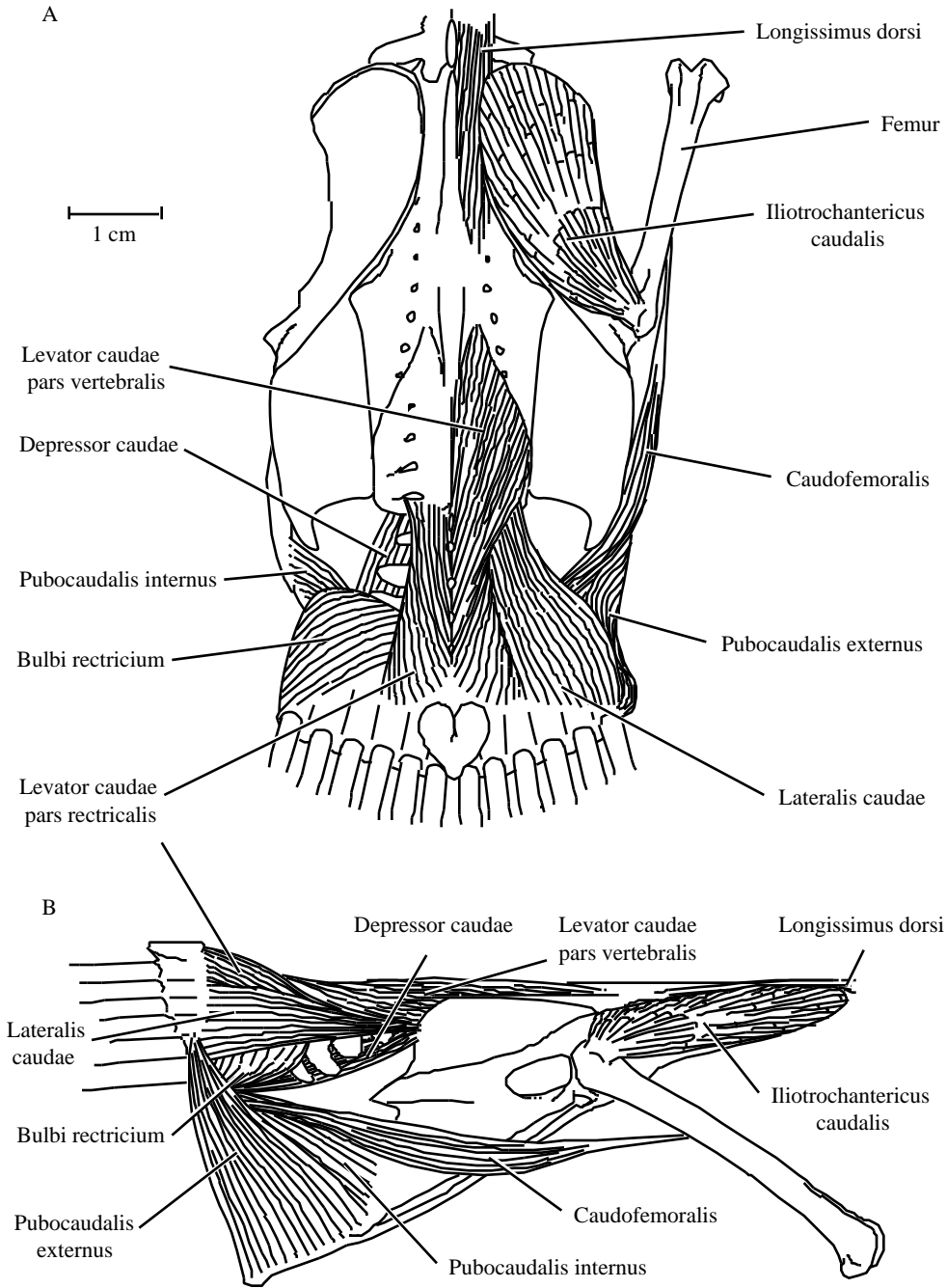


Fig. 2

Fig. 2. Anatomy of the caudal region of the pigeon, *Columba livia*. (A) Dorsal view of the pelvis and tail. Superficial caudal muscles are shown on the right along with the longissimus dorsi, an epaxial muscle of the trunk, and two leg muscles, the iliотrochantericus caudalis and caudofemoralis. Deeper tail muscles are shown on the left after the removal of the overlying levator caudae pars vertebralis, lateralis caudae and pubocaudalis externus (redrawn after Baumel *et al.* 1990). (B) Right lateral view of the superficial caudal muscles. In both views the overlying transversus cloacae muscle has been removed.

Tail kinematics

Representative movements of the tail during liftoff and the three flight modes are shown in Figs 3 and 4. In the transition from terrestrial to aerial locomotion the tail undergoes dramatic changes in orientation (Fig. 3). When the bird is standing, the tail is typically furred (rectrices adducted) and slightly tented (concave down; Fisher, 1946; Baumel, 1988). As the wings are raised, the tail elevates, flares and arches (concave up). The tail is depressed during the first downstroke and remains highly flared. This general position is maintained into takeoff (Fig. 4A). In this mode, the tail is slightly adducted as the wings pass by the rectrices during the downstroke and then abducted again during the upstroke. In comparison to takeoff, both the body and tail are oriented closer to the horizontal in slow level flight (Fig. 4B). As birds approach the perch to land, the body axis once again become more vertical; the tail is highly flared during landing (Fig. 4C).

Walking

During walking (Figs 5A, 6; Table 2) the pectoralis and the majority of caudal muscles are inactive. The iliотrochantericus caudalis is active from late in the swing phase through most of the propulsive phase of the stride cycle. This activity is similar to that known for other avian species (Gatesy, 1989; Jacobson and Hollyday, 1982). During walking, the caudofemoralis (Fig. 6) shows either no activity (below approximately 2strides s^{-1}), low-amplitude activity in the mid-late propulsive phase (from about 2–3strides s^{-1}) or high-amplitude activity (above 3strides s^{-1}). The longissimus dorsi is activated continuously, but within the sustained activity its EMG exhibits a biphasic modulation of amplitude with each stride. It is clear from bilateral implants that this modulation of trunk epaxial EMG amplitude is relatively symmetrical. Within the tail, only the levator caudae pars vertebralis and pars rectricalis show a consistent EMG during terrestrial locomotion. These muscles fire one burst per stride, with pairs alternating their activity in phase with the striding legs. Caudal hypaxials are typically inactive during walking.

Liftoff

Birds move from terrestrial locomotion to flight during liftoff by initiating the first wingbeat and pushing off the ground with the legs (Figs 3, 5B, 6; Table 2). A preparatory period of leg and tail activity precedes the onset of activity in the pectoralis, but all muscles recorded exhibit pronounced activity during this explosive locomotor behavior. Activity normally appears first in the hypaxials; this continues through the first downstroke. Multiple bursts of EMG activity in the pubocaudalis externus and internus cannot be compared easily between trials and birds. The onset and offset of this collective activity are given in Table 2 and Fig. 5B. The depressor caudae has three EMG bursts per

liftoff. The leg and epaxial muscles typically become active as the wing begins to elevate. The ilipectoralis caudalis and caudofemoralis fire relatively simultaneously during pushoff and cease activity prior to the initiation of the first downstroke. The longissimus dorsi and the caudal epaxials continue their activity through the upstroke/downstroke transition. All but the levator caudae pars rectorialis have a second burst late in the

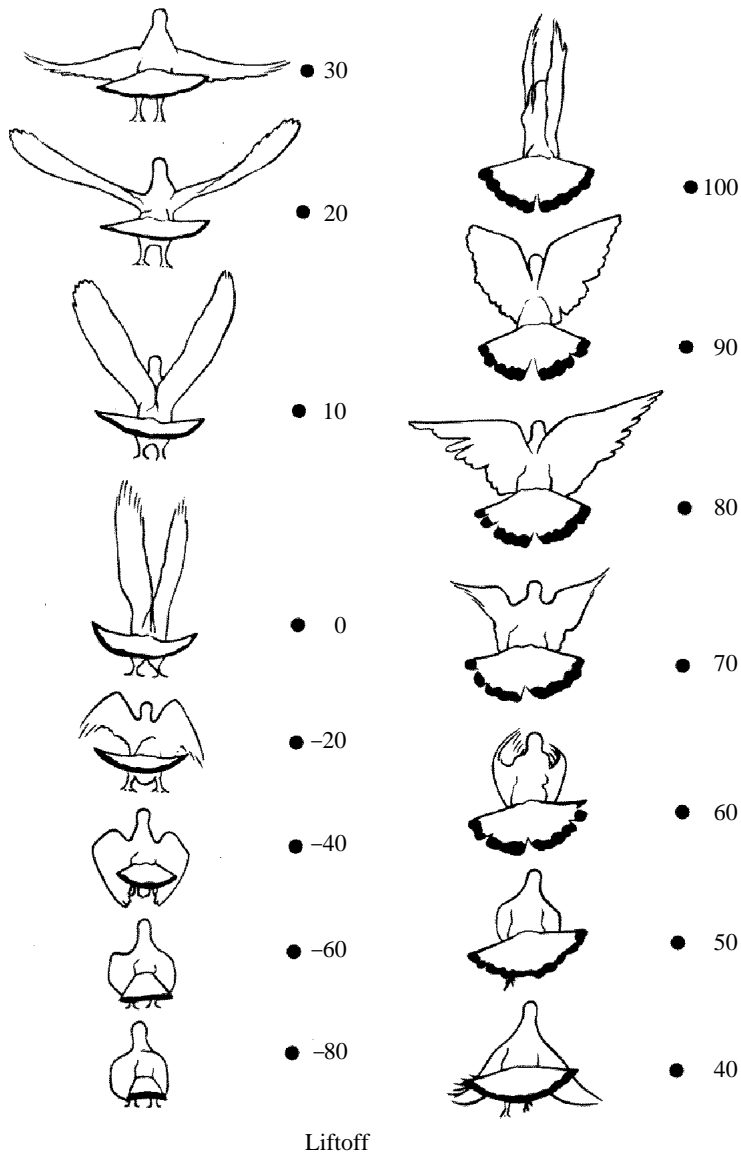


Fig. 3. Kinematics of a pigeon during liftoff filmed at 200frames s^{-1} in posterior view. Timing (ms) is shown relative to time zero at the beginning of the first downstroke. The sequence begins at the lower left (80ms prior to downstroke), proceeds up the page and continues in the second column. The complete wingbeat cycle lasts 100ms. The black dots mark a stationary point on the floor.

downstroke. The tail is elevated and flared as the wings are raised and then depressed as the wings descend. The bulbi retractor was activated just prior to the pectoralis in the one liftoff recorded for this muscle. The feet usually leave the ground during the second half of the downstroke, but the exact timing of last contact is somewhat variable.

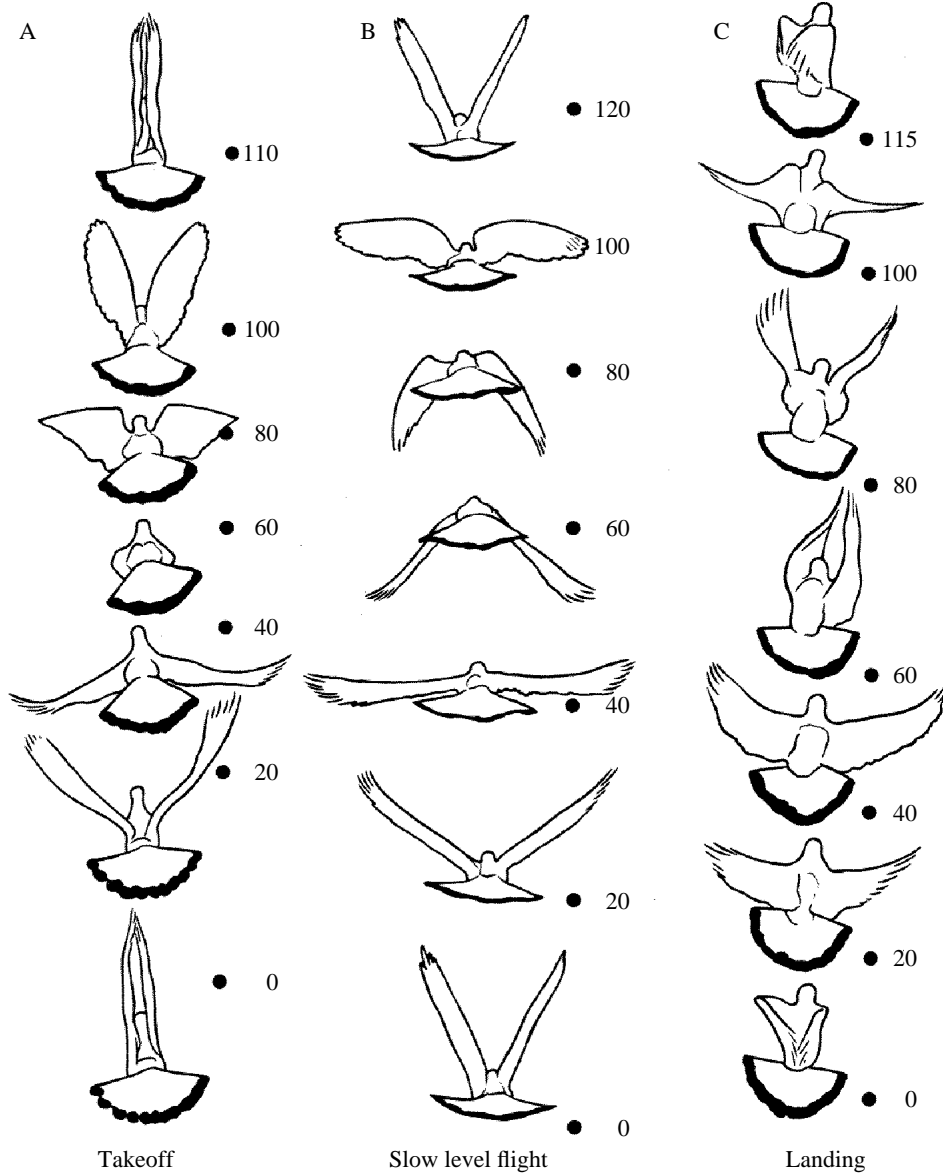


Fig. 4. Kinematics of a pigeon for one complete wingbeat cycle of (A) takeoff, (B) slow level flight and (C) landing flight modes in posterior view. Each sequence begins at the bottom of the page at the start of the downstroke at time zero. The black dots mark a stationary point on the floor in takeoff, at the end of the flight corridor in level flight and below the perch-platform in landing. Wingbeat cycles lasted 110, 120 and 115ms, respectively.

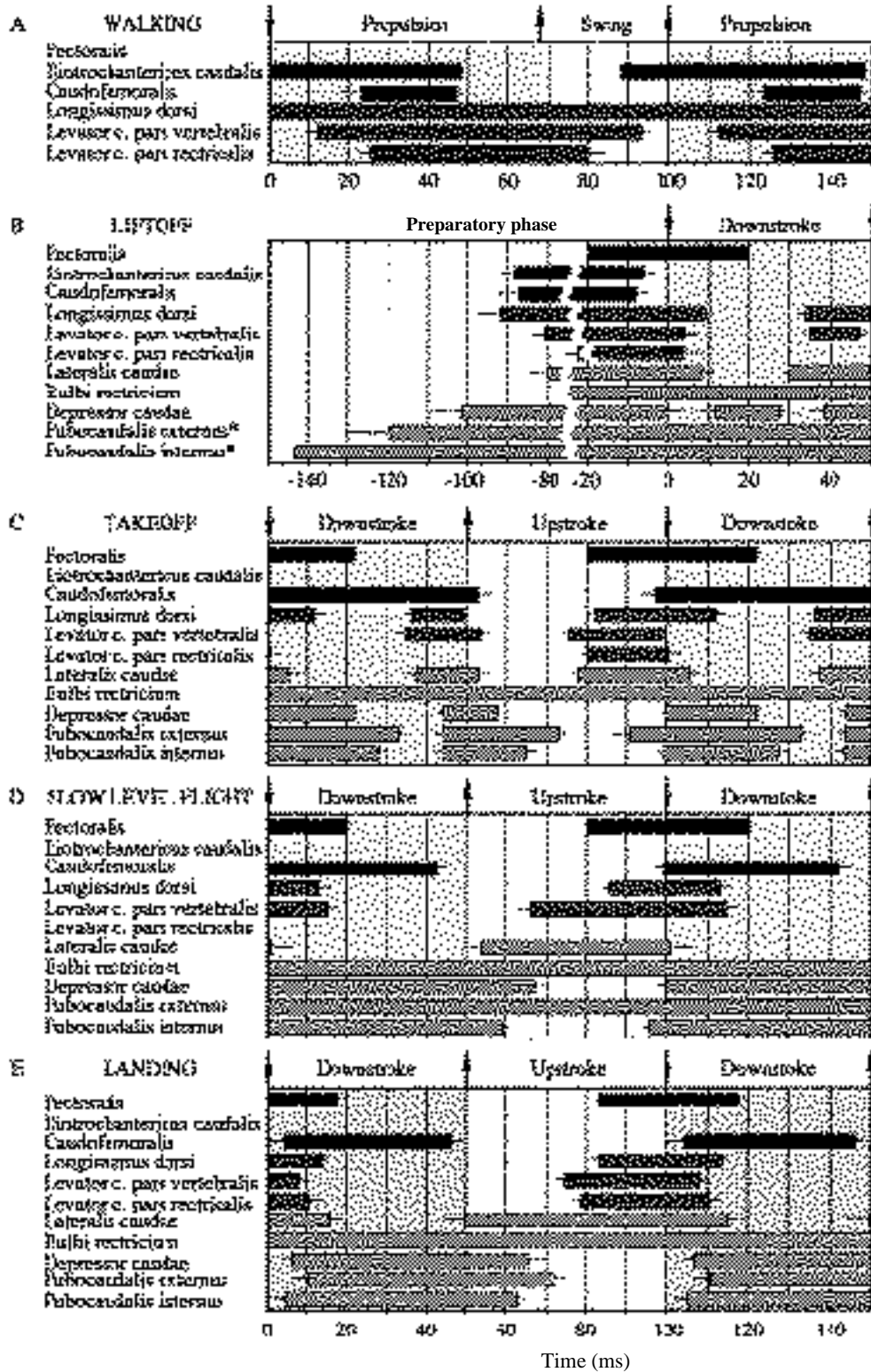


Fig. 5

Fig. 5. Summary diagrams of EMG activity in selected muscles of the pigeon during five modes of locomotion: (A) walking, (B) liftoff, (C) takeoff, (D) slow level flapping flight and (E) landing. Bars indicate the mean onset and offset (and s.e.) of EMG activity normalized to the stride or wingbeat cycle. One and a half cycles (150%) are shown for each mode except liftoff, in which a period of the preparatory phase has been removed. Limb muscle activity bars are filled in black, epaxial muscles in dark grey and hypaxials in medium grey. The propulsive phases of walking and the downstroke phases of flight are shown by a lightly shaded background. Arrows indicate footfall pattern or the beginning of downstroke and upstroke. Muscles marked with an asterisk show multiple bursts within the onset and offset times shown. The single liftoff EMG from the bulbi rectricium began 35% before the downstroke. Cycle durations for each mode are given in Table 1.

Takeoff

During takeoff (Figs 4A, 5C; Table 2) and other flight modes the pectoralis is active to decelerate the elevating wing and provide the major power for the downstroke (Dial *et al.* 1988). The ilirotrochantericus caudalis is usually inactive, but may show a brief, bilateral burst of EMG activity during the downstroke. Caudofemoralis EMG activity is also seen during the downstroke, but is of much lower intensity than in fast walking or liftoff (Fig. 6). Variation in leg muscle activity appears to depend on the orientation and movement of the legs during flight, which often differs among individuals. Most other muscles are active twice in each wingbeat. The longissimus dorsi is active at the upstroke/downstroke transition and again in late downstroke (Fig. 7). The levator caudae pars vertebralis (Fig. 7) and lateralis caudae show bursts of activity in late upstroke and late downstroke. The levator caudae pars rectricialis differs from these in that it has only a single (late upstroke) burst of activity (Fig. 8). Activity is continuous in the bulbi rectricium. The depressor caudae, pubocaudalis externus (Fig. 9) and pubocaudalis internus are active in early downstroke and during the downstroke/upstroke transition.

Slow level flapping flight

Once birds achieve slow level flapping flight, either from unassisted takeoff or after hand release, most muscles show only a single EMG burst per wingbeat (Figs 4B, 5D; Table 2). The pectoralis continues to power the wing, but compared to takeoff there is a pronounced reduction in its EMG amplitude (Dial *et al.* 1988). The ilirotrochantericus caudalis is typically inactive. Caudofemoralis EMGs of low amplitude occur during the downstroke. Longissimus dorsi activity is reduced from its biphasic takeoff pattern to a single burst per wingbeat near the upstroke/downstroke transition (Fig. 7). Similarly, the levator caudae pars vertebralis and lateralis caudae show single bursts of activity, primarily during the upstroke. The levator caudae pars rectricialis, which has a single burst of activity during takeoff, becomes completely inactive during level flight (Fig. 8). The bulbi rectricium continues to be active throughout the wingbeat cycle. The dual bursts seen in the depressor caudae and pubocaudalis internus during takeoff merge into a single downstroke burst during each cycle of level flapping flight. Activity in the pubocaudalis externus is continuous rather than in discrete bursts, with some modulation of EMG amplitude (Fig. 9).

Table 2. Summary of timing of pigeon wing, leg, trunk and tail muscle activity during five locomotor modes

Muscle	Walking	Liftoff	Takeoff	Slow LFF	Landing
Pectoralis	–	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
	–	39.4±0.6	41.7±1.0	39.3±1.2	34.8±2.6
Iliotrochantericus caudalis	0.0±0.0	–68.3±2.9	–	–	–
	60.3±0.9	13.7±3.8	–	–	–
Caudofemoralis	34.8±4.8	–67.1±5.4	16.5±2.9	17.9±1.6	21.4±5.1
	58.9±2.1	11.5±3.3	72.7±3.3	61.5±3.5	63.3±2.7
Longissimus dorsi	0.0±0.0	72.5±5.1	1.7±1.4	4.2±1.1	0.0±2.2
	100.0±0.0	28.9±1.9	31.7±2.7	31.9±3.2	30.8±1.5
		53.6±1.5	56.0±1.3		
Levator c. pars vertebralis	23.7±2.4	–61.4±2.6	–4.7±1.4	–15.2±2.8	–8.5±2.0
	104.9±2.4	23.9±3.4	18.3±1.9	33.9±3.3	25.0±1.9
		54.7±1.3	54.5±2.0		
		67.0±2.1	73.2±2.1		
Levator c. pars retricalis	37.1±2.3	–52.7±2.4	0.0±1.0	–	–4.4±1.7
	91.6±3.8	23.4±4.9	20.3±3.1	–	27.2±3.3
Lateralis caudae	–	–60.2±4.3	–2.5±1.7	72.4±3.0	66.7±5.2
	–	28.2±3.0	25.4±2.5	119.9±5.9	132.3±3.8
		49.7±1.3	57.1±2.3		
Bulbi rectricium	–	–35.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
	–	100.0±0.0	100.0±0.0	100.0±0.0	100.0±0.0
Depressor caudae	–	–81.7±7.5	19.3±0.7	18.8±2.4	23.4±2.2
	–	19.0±5.4	41.8±0.5	85.9±2.8	82.4±4.3
		31.5±3.5	63.9±1.1		
		47.7±1.8	77.2±2.6		
		58.0±2.5			
Pubocaudalis externus	–	–99.5±10.2*	10.7±3.9	0.0±0.0	27.3±3.8
	–	98.1±3.3*	53.0±1.1	100.0±0.0	89.0±3.1
			63.7±1.8		
			93.1±2.0		
Pubocaudalis internus	–	–123.4±12.6*	18.9±1.5	14.5±1.3	21.8±2.6
	–	88.1±1.3*	47.4±2.2	78.3±1.4	79.9±1.9
			63.6±1.8		
			84.8±2.7		

Stride and wingbeat cycles were normalized to 100%, beginning with time zero at the onset of the firing of the iliiochantericus caudalis and pectoralis, respectively.

The relative onset and offset times and standard errors are shown for each burst (some muscles have more than one burst).

Dashes indicate that the muscle is normally inactive in that mode. Asterisks signify highly variable bursting between the onset and offset values.

Values are mean ± S.E.

Landing

The pattern of muscle activity during landing (Figs 4C, 5E; Table 2) is similar but not identical to that during slow level flapping flight. Pectoralis EMGs increase in amplitude

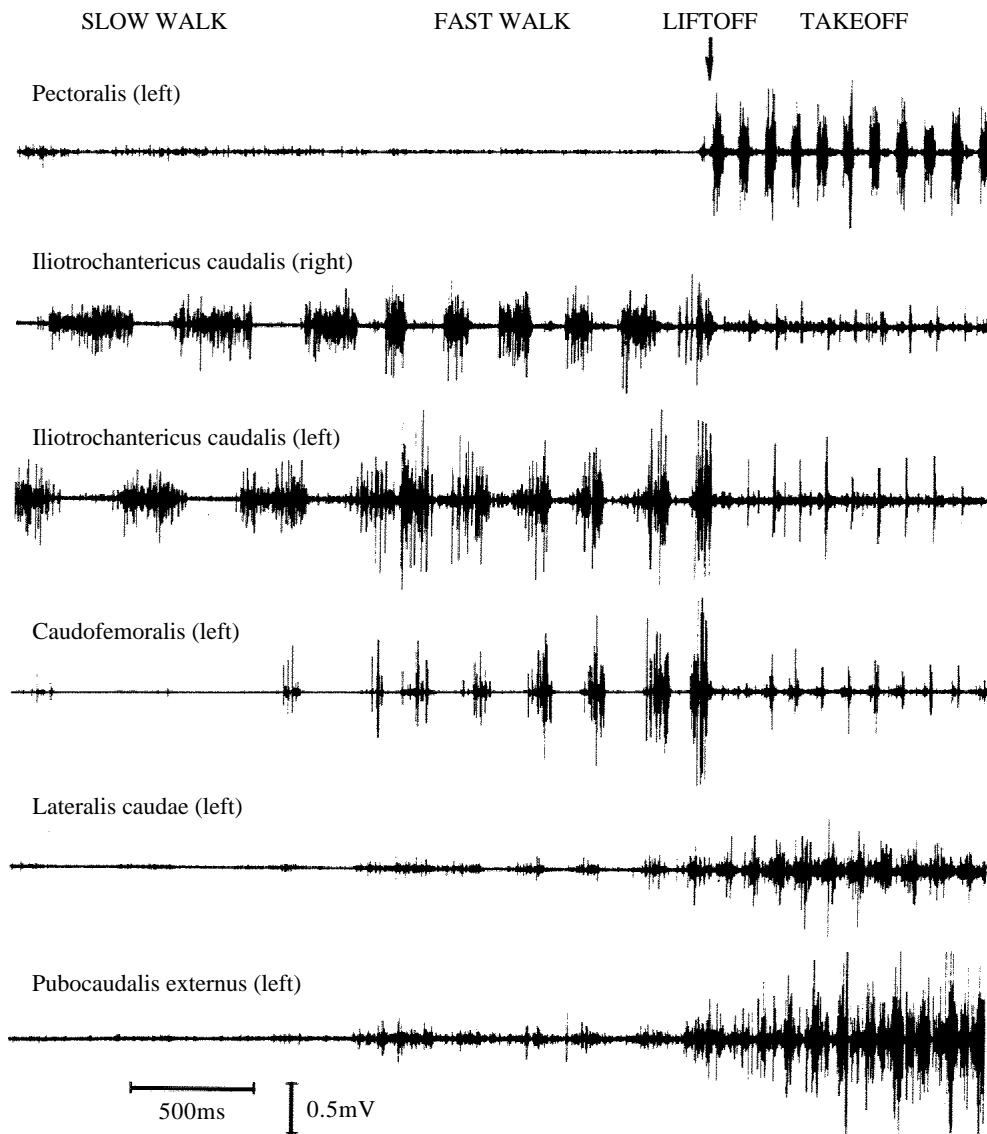


Fig. 6. Simultaneously recorded muscle activity in selected wing, leg and tail muscles of the pigeon during a terrestrial-to-aerial sequence of locomotion. In slow walking, the right and left leg muscles are activated alternately with each step; the pectoralis and most tail muscles are inactive. As the bird shifts to a faster walking speed, stride frequency increases and the caudofemoralis becomes active. At liftoff, all muscles fire as the bird launches upwards. Once it is airborne, the pectoralis and other tail muscles show high-amplitude activity. Bursts of activity in the ilioprochantericus caudalis are often absent or become reduced as birds enter slow level flight.

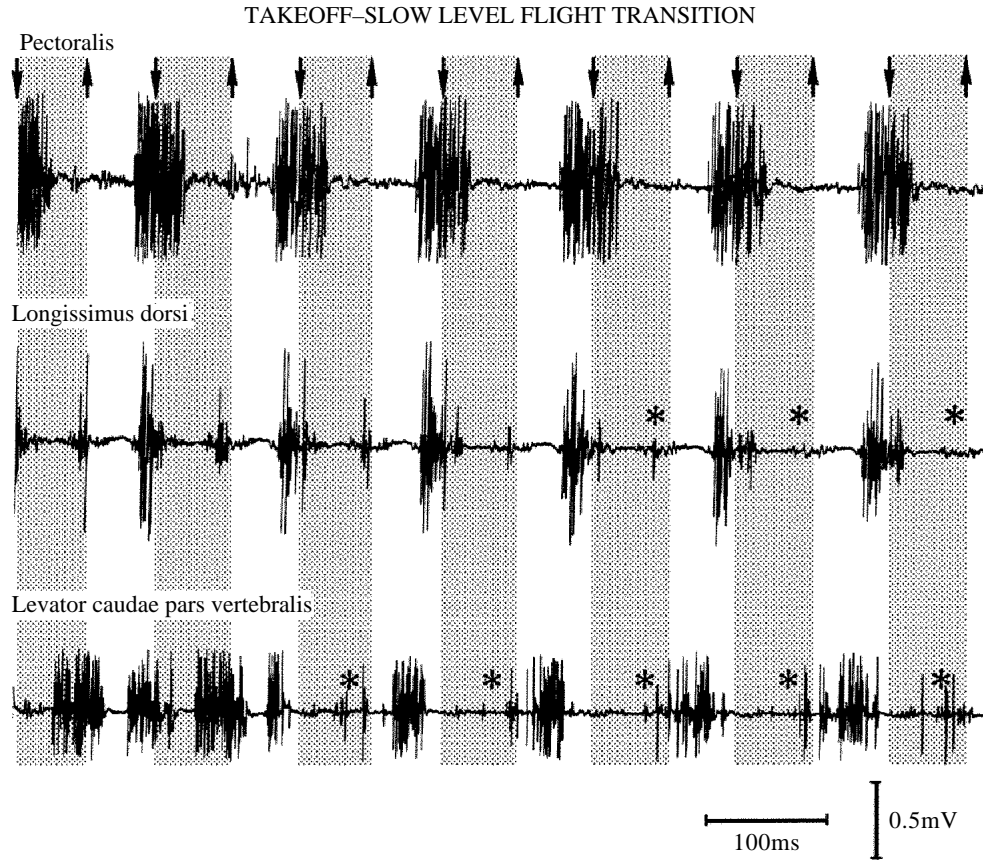


Fig. 7. Electrical activity of the pectoralis (wing), longissimus dorsi (trunk) and levator caudae pars vertebralis (tail) recorded simultaneously during the transition from takeoff to slow level flight modes. The bird shifts from takeoff mode to slow flight mode over several wingbeats. Note that the longissimus dorsi and levator caudae pars vertebralis have two bursts of EMG activity during each wingbeat during takeoff (start of figure). As the bird shifts to slow level flight (end of figure) the late downstroke burst is lost (*). Also note that these adjacent epaxial muscles have different activity patterns. Downstroke is shaded. Arrows show the beginning of the downstroke and upstroke phases of the wingbeat cycle.

as birds slow down to land, while the caudofemoralis typically retains its level-flight activity. Within the tail, the levator caudae pars rectricalis, which is silent in the level flight mode, is active near the upstroke/downstroke transition during landing (Fig. 8). EMG activity in the bulbi rectricium remains continuous, but fluctuates in amplitude, being highest during the downstroke. Activity in the pubocaudalis externus (Fig. 9) is reduced from its continuous level flight pattern to a downstroke burst similar to that of the depressor caudae and pubocaudalis internus.

Trends in muscle activity

The limb muscles we sampled exhibit high-intensity co-activity only during liftoff, when the bird makes the transition between terrestrial and aerial locomotion. The

LEVATOR CAUDAE PARS RECTRICALIS

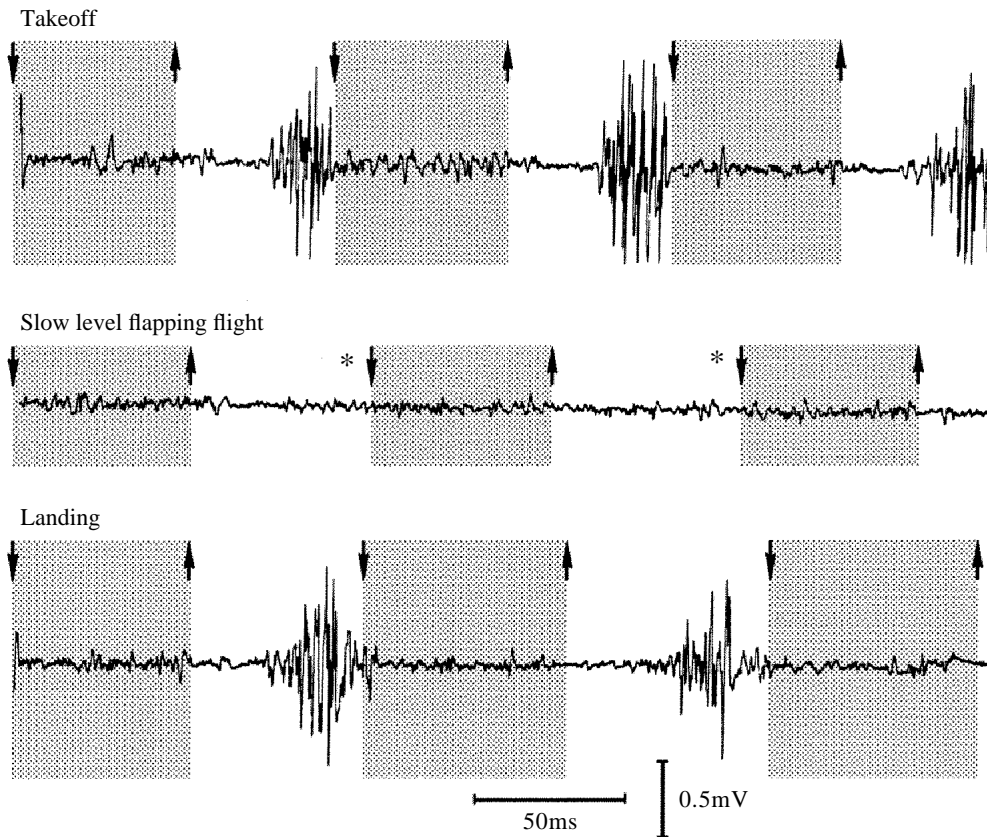


Fig. 8. Modulation of activity in the levator caudae pars rectorialis among different modes of flight. These sequences from a single trial show clear EMG bursts in the second half of the upstroke during takeoff and landing, but no significant activity during slow level flight (*). We interpret the low-level signal in slow level flight and between bursts in takeoff and landing as background activity not associated with functioning of the implanted muscle. Downstroke is shaded. Arrows show the beginning of the downstroke and upstroke phases of the wingbeat cycle.

pectoralis is silent during walking but active during flight. When walking, the iliopsoas and caudofemoralis burst with each stride. During flight, these hindlimb muscles have activity that, when present, is of lower amplitude than during terrestrial modes (walking and liftoff).

Within the epaxial musculature, activity often differs among the longissimus dorsi, levator caudae pars vertebralis and levator caudae pars rectorialis. All epaxials are active during walking. In this mode the longissimus dorsi exhibits continuous activity with bilaterally symmetrical fluctuations in EMG amplitude twice per stride. Both the levator caudae pars vertebralis and pars rectorialis have monophasic EMGs. The right and left levator caudae alternate in activity in phase with the ipsilateral striding hindlimbs. During liftoff and takeoff, the longissimus dorsi and levator caudae pars vertebralis fire twice per

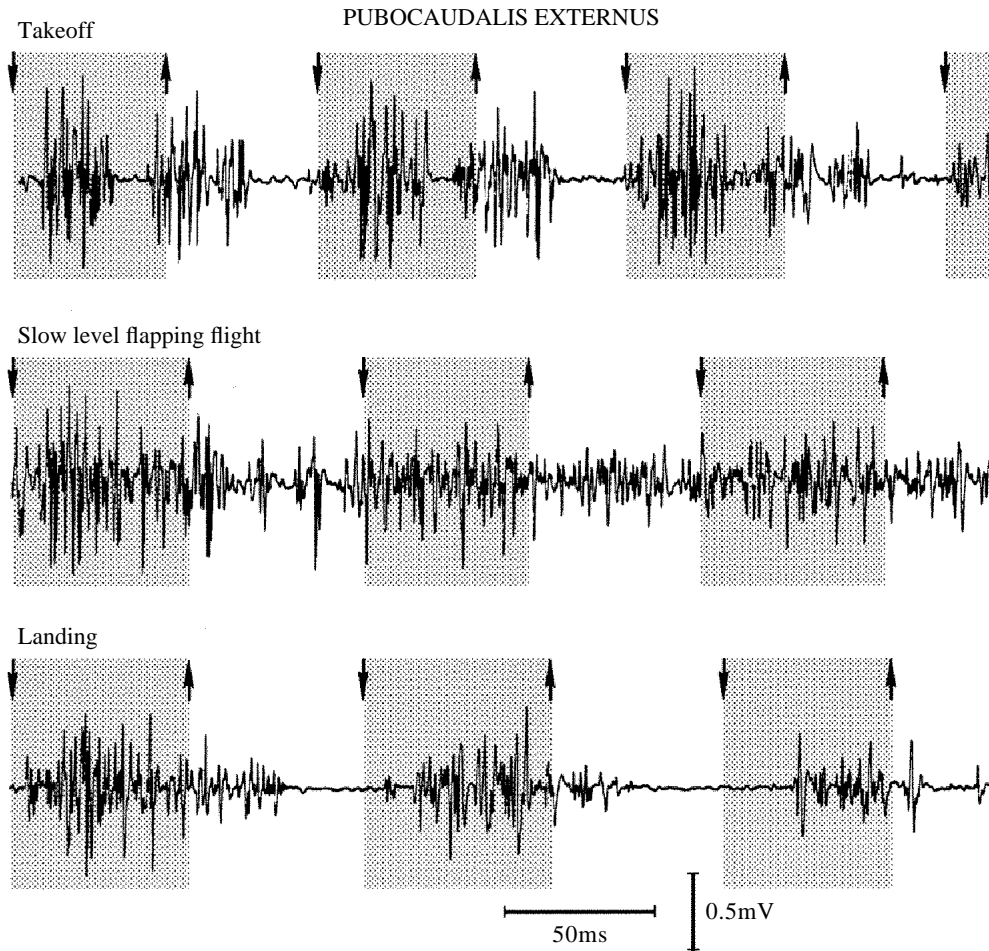


Fig. 9. Activity modulation in the pubocaudalis externus among different flight modes. These sequences from a single trial show that this muscle has biphasic activity during takeoff, which merges into continuous EMG activity in slow level flight. During landing, the pubocaudalis externus is active once per wingbeat. Downstroke is shaded. Arrows show the beginning of the downstroke and upstroke phases of the wingbeat cycle.

wingbeat, while the levator caudae pars rectorialis fires only once. In the transition to slow level flight, each epaxial loses one burst of EMG. Those that have a biphasic EMG during takeoff become monophasic (Fig. 7); the levator caudae pars rectorialis turns off completely (Fig. 8). Activity in the levator caudae pars vertebralis begins prior to that in the longissimus dorsi and pars rectorialis in most modes.

Many motor patterns are present among hypaxial muscles. The lateralis caudae, bulbi rectorium, depressor caudae, pubocaudalis externus and pubocaudalis internus are normally silent during walking. Once activated during liftoff, the bulbi rectorium remains active continuously during takeoff, level flight and landing. Other hypaxials exhibit at least two EMG bursts during liftoff and takeoff. As birds shift to slow level

flight these dual takeoff bursts merge. The pubocaudalis externus is unusual in that it is continuously active (Fig. 9), whereas the lateralis caudae, depressor caudae and pubocaudalis internus burst phasically.

Discussion

Baumel (1988) concludes his monograph on the pigeon tail by stating the need for more investigations of tail use and tail muscle activity during flight. The present study, combining electromyography and high-speed cinematography, provides initial experimental data on the neural control of caudal muscles during locomotion. Our data reveal that the pigeon's major tail muscles exhibit phasic patterns of cyclical activity synchronized with either wing or leg movement. However, not all muscles are active in all modes, particularly walking. The most dramatic example of inactivity may be the levator caudae pars rectricalis, which is active during all locomotor modes studied except slow level flight. In the slow level flight mode, therefore, the levator caudae pars rectricalis does not normally contribute to tail control. The EMG activity pattern of this and other muscles is critical to understanding their function, but is not readily predictable from anatomical or kinematic information. The temporal patterns of EMG activity presented in this paper do not delineate muscle function conclusively, but set limits on the interpretation of each muscle's contribution to the control of tail movement.

Modulation of EMG timing with locomotor mode

Our measurements of tail muscle activity differ significantly from those found for wing muscles of pigeons performing equivalent flight behaviors under identical conditions (Dial, 1992a). Fifteen of sixteen muscles of the wing showed only slight changes in timing of EMG activity between takeoff, slow level flapping flight, landing, ascending and descending (Dial, 1992a). All wing muscles studied were active in every mode and retained the same pattern of mono- or biphasic activity during takeoff, slow level flapping flight and landing. In contrast, the majority of tail muscles exhibit conspicuous changes in the timing of their activity during these same flight modes. The motor pattern of many muscles varies from no activity to a single burst, a double burst or a continuous burst of EMG activity for each cycle of limb movement in different locomotor modes.

We suggest that the birds have evolved different neuromuscular control patterns for their forelimb and tail flight surfaces (Fig. 10). The difference in the complexity of timing in the tail (modulated) and wing (stereotypic) may stem from the need to standardize control signals in the rapidly oscillating forelimb. Perhaps only a single temporal motor pattern evolved in the flapping wing as the degrees of freedom in the elbow and wrist were reduced during the origin of avian flight. This basic pattern, in conjunction with an automatic linkage system in the wing (Headley, 1895; Fisher, 1957; Dial, 1992b), forms the basis for steady-state flapping flight. Alterations of wing shape during non-steady flight modes appear to be controlled by varying the intensity of forelimb muscle activation (Dial, 1992a). In addition, complex changes in wing movements may be controlled proximally by the differential recruitment of subvolumes of the pectoralis (Dial *et al.* 1988; Dial, 1992b; D. F. Boggs and K. P. Dial, in preparation).

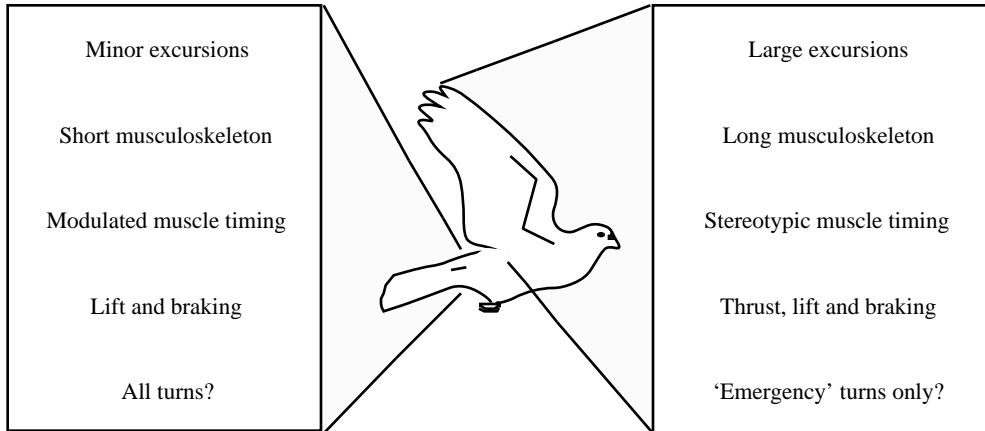


Fig. 10. Summary of differences between, and contributions of, the wing and tail during flight. The relative significance of caudal and forelimb flight surfaces in turning and other maneuvers is still unknown.

Unlike the wing, the tail does not undergo dramatic oscillations during flight and so may be free of a constraint to standardize temporal activation of its musculature. Although we did not quantify EMG intensity in this study, tail muscles clearly exhibit changes in both timing and intensity (S. M. Gatesy and K. P. Dial, unpublished data). This flexibility in caudal motor pattern between different modes of forward, non-turning flight may reflect the versatile role of the tail in locomotion. Certain types of flapping flight appear to require more contribution from the tail than others, but the wings are always in use and are therefore less likely to vary. One point that should be stressed is that tails of pigeons flying in our corridor were always at least slightly flared and depressed. This has been referred to as 'slow flight' by Brown (1948, 1963) and Simpson (1983). In fast flying pigeons in the wild, the tail is primarily adducted (furled) and held parallel to the body axis (Pennycuick, 1975; personal observation). We predict that during fast, non-turning level flight the tail is held by aerodynamic rather than muscular forces and that activity of caudal muscles is greatly reduced. This would be consistent with the activity of the levator caudae, which is inactive in slow level flight; other muscles may similarly be turned off as birds achieve higher speeds.

Segregation of the avian locomotor system

Most birds are considered to have two relatively independent locomotor systems: the wings for flight and the legs for walking, running and hopping (Pennycuick, 1986; Butler, 1991). This distinction between aerial and terrestrial locomotor systems is clearly illustrated in our simultaneous recordings from the pectoralis (wing) and ilirotrochantericus caudalis (leg) during different locomotor modes (Fig. 6). The wing muscle is inactive when the bird is walking with alternating leg movements. Once airborne, the leg muscle is typically inactive as the bird flies with synchronous wingbeats. Much of the leg activity appears to be related to restraining the folded hindlimbs against the bird's body during takeoff, when they may be experiencing more violent

forces than those in level flight. Clearly, there must be some leg muscle activity (possibly in tonic fibers) to keep the legs flexed during flight, but we predict that this will be minor compared to that when the bird is moving on the ground. We cannot rule out the possibility of subthreshold excitation of motoneurons of muscles that we identify as inactive; this will have to be shown neurophysiologically.

The activity of caudal muscles supports the hypothesis that in the pigeon the tail has its primary allegiance to the wings rather than to the legs in this segregated locomotor system (Gatesy and Dial, 1991). Coordination of the tail and forelimbs during flapping and gliding (e.g. Tucker, 1992) is not surprising, but there is no evidence to suggest that this type of integration was present in the bipedal theropods that gave rise to birds. The tail's primitive linkage is to the hindlimb and trunk, as found in living saurians such as lizards and crocodylians (Gatesy, 1990). What changes accompanied the tail's unprecedented affiliation with the forelimbs?

There is anatomical and functional evidence that the tail has been decoupled during the evolution of birds from their theropod ancestors. Muscular connections have been eliminated or weakened so that the tail is almost completely independent from the trunk and hindlimbs (Fig. 2). This decoupling appears to have permitted the tail to specialize for the control of the tail feathers during flight and form a novel association with the wings. Verification of this decoupling can be found in each major muscle group of the tail. First, the epaxial musculature is no longer continuous along a bird's dorsal surface. There is a distinct gap between the longissimus dorsi in the trunk and the levator caudae pars vertebralis in the tail. This anatomical segregation coincides with differences in motor pattern during locomotion; the caudal epaxials are not acting as simple segmental extensions of the trunk musculature. Second, the caudal hypaxials of walking pigeons are inactive so that their involvement in terrestrial locomotion, if any, must be passive. This differs from *Alligator*, in which there is both epaxial and hypaxial activity in the tail during walking (S. M. Gatesy, unpublished data). Third, pigeons walk at low speeds without using the caudofemoralis. The avian caudofemoralis is either reduced (relative to saurians) or completely lost (George and Berger, 1966) and is no longer a crucial element in powering the limb. In contrast, this muscle forms the basis of hindlimb retraction in crocodylians, lizards and, presumably, the dinosaurian ancestors of birds (Gatesy, 1990). In the pigeon, a small remnant of the tail's primitive role can be seen in the alternating activity of the levator musculature during walking.

Subdivision of the caudal epaxial musculature

Past workers have often divided the caudal epaxial musculature into two muscles (Shufeldt, 1890; Fisher, 1946; George and Berger, 1966), but recently Baumel (1988) reunited them as two parts (pars proximalis and pars distalis) of a single muscle called the levator caudae. This nomenclature will be changed once again (pars vertebralis and pars rectricialis) to help make these names more informative (Baumel *et al.* 1993). Although the fascicles of these two parts are oriented in parallel, their insertions and apparent actions differ. Our EMG data confirm that these muscular subdivisions are not used in the same way during locomotion. For example, the levator caudae pars vertebralis fires two bursts per wingbeat during takeoff, whereas the pars rectricialis fires only one. In slow

level flapping flight, the levator caudae pars vertebralis fires one burst per wingbeat, but the pars rectorialis is completely silent. It is hoped that the new terminology will reflect the heterogeneity within the levator caudae and not imply uniformity.

Functional interpretation

The EMG results presented here are a prerequisite for an understanding of tail function during locomotion. For example, EMG data help confirm the bulbi rectorium as an abductor of the rectrices, as predicted by Baumel (1988). The continuous activation of these paired muscles holds the tips of the calami of the rectrices together, thus maintaining the tail fan seen during flight (Figs 3, 4). The lateralis caudae musculature may assist the bulbi rectorium initially, but its phasic activation does not seem adequate to sustain the abducted position.

The relationship between the activity of caudal muscles and tail movement, however, is not always clear. Although we have not presented a quantitative kinematic analysis, our overall conclusion is that the tail is relatively stable during most wingbeats. Fluctuations in elevation/depression and abduction/adduction do occur, but these do not always have a one-to-one correspondence with the activity of caudal muscles. In takeoff, for example, the tail does not undergo observable pulsatile movements for each burst of biphasic activity. It is not known, however, to what extent caudal muscles continue to produce force after the cessation of EMG activity; this lag could act to smooth the kinematic output generated by punctuated activation.

We hypothesize that much of the EMG activity of caudal muscles is related to fixing tail position for appropriate aerodynamic presentation as the oscillating wings impose dramatic forces on the body. The coactivation of epaxials and hypaxials near the downstroke/upstroke transition during takeoff may stabilize the tail during this relatively violent movement. Unfortunately, the interaction of aerodynamic, inertial and muscular forces during takeoff and other flight modes is not understood. This makes the interpretation of caudal muscle function particularly difficult, since tail kinematics are likely to be the net result of all of these forces, not just of muscular activation.

Future work

Although we attribute the majority of tail muscle activity to stabilization, we cannot distinguish between modulated output from a central pattern generator and reflex reactions to body and tail movement. Both of these sources may be involved in the motor output we record from the tail musculature. Further research is needed to identify the nature of caudal muscle activity and its integration with the forelimb spinal locomotor networks.

We suggest that a better perception of caudal muscle function will come through studies of more complex flight behaviors. In turning flight, for example, the tail moves asymmetrically as the bird maneuvers (Fig. 10). This kinematic asymmetry is presumably initiated, maintained and terminated by differential activation of contralateral pairs of caudal and wing muscles. It is likely that the muscle activity during slow level turning flight will be similar to that during slow level non-turning flight, but with

variations in timing and/or intensity creating asymmetries during the maneuver. Using non-turning EMGs as baseline signals may reveal the differences in activity that make the tail deviate during turning. Correlating these differences with tail movement may then lead to a clearer understanding of tail muscle function, the relative contributions of the wing and tail in turning, and the evolution of vertebrate flight.

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